TORSION STUDIES IN TWINING PLANTS

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(WITH SIX FIGURES)

Introduction

This paper deals with a certain phase of the physiology of twining plants. It is an account of some experiments upon the scarlet runner or flowering bean (*Phaseolus multiflorus*) and the black or corn bindweed (*Tiniaria Convolvulus* [L.] Webb and Moq.), in which a modified form of auxanometer was used. To a limited extent the hop (*Humulus Lupulus* L.) was studied also.

The attention which twining plants have received from many observers has resulted in considerable literature on the subject. The main facts, however, have been well summarized by Vines[1] and by Pfeffer.[2] A résumé of these accounts seems unnecessary for our present purpose, but it is convenient, as well as in accord with the views of these workers, to consider the phenomenon as involving the following as its most striking factors: (1) circumnutation of the growing tip; (2) winding of the stem about its support; (3) torsion of the stem in the same direction as the winding (homodromous); (4) torsion in the opposite direction (antidromous). The relation of these factors to one another is not perfectly understood, and I shall not enter into any discussion regarding it. This paper deals only with torsion of the stem.

Not having ready access to the literature, the aid of Mr. Peter J. Klaphaak, of the University of Michigan, was secured in looking up references, and I desire to express my appreciation of his services. In as extensive a review as it was possible to make, no reference was found to any method of approaching the problem similar to the one here described.

[1] Vines, S. H., Lectures on physiology of plants. 1886.

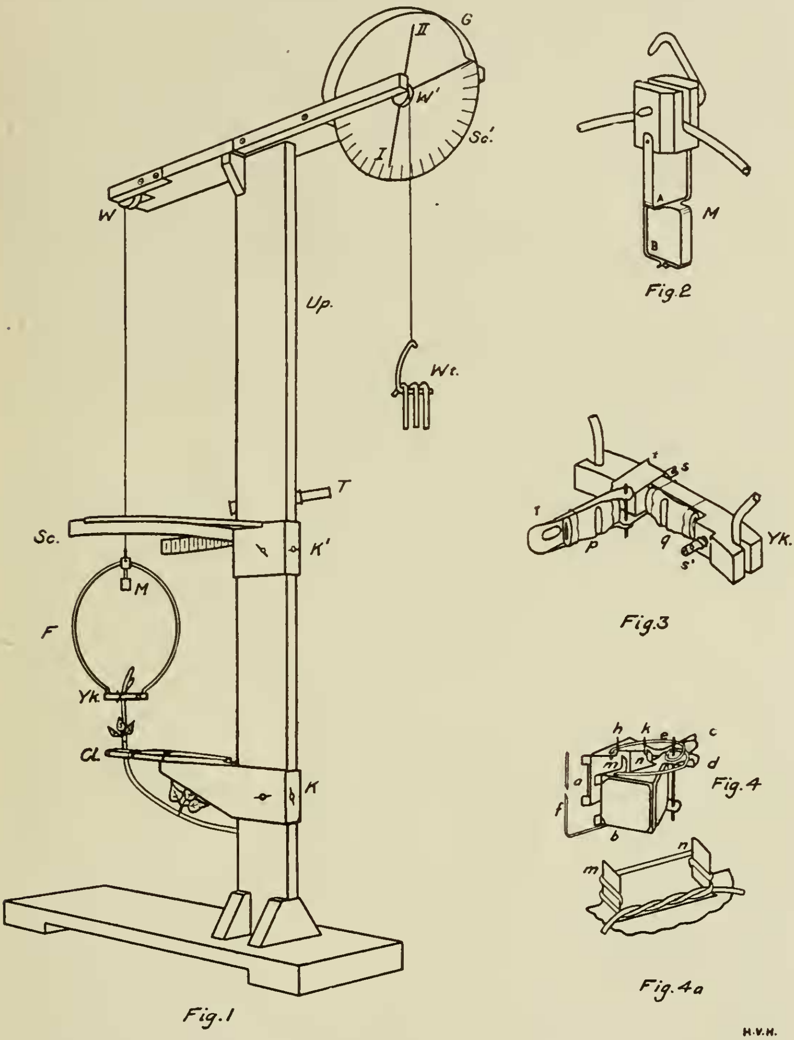
[2] Pfeffer, W., Physiology of plants, translated by A. J. Ewart, Vol. III. 1906.

Method

The method consisted in stretching vertically a growing internode, or parts of two adjacent internodes, and measuring the amount of twist and the corresponding length. The object of this stretching is, while giving support, to eliminate twining proper, and the amount of stretching is slightly greater than that required to accomplish this. An estimate of the torsional rigidity at different lengths was also made. In certain experiments I have compared this with the diameter and with the amount of lignification. I have also begun studies on antidromous torsion, and have made a few other observations.

The apparatus is illustrated in figs. 1–4. There stands on a base an upright (*Up*) about 1 m. high. This has a top piece bearing two wheels (*W* and *W'*), over which runs a fine silk thread. On the upright are also two sliding clamps (*K* and *K'*), which can be secured at any height. The lower of these (*K*) has an arm bearing a special kind of clamp (*Cl*) for holding the lower part of the growing internode. The other (*K'*) carries a telescope (*T*) and a semicircular scale (*Sc*), which is graduated on the inside so as to read half-degrees. I found 28 cm. a convenient diameter for this scale. The upper part of the internode used is held by the frame (*F*), which is suspended by the silk thread already mentioned. The weight (*Wt*) supplies the proper amount of tension. By means of the scale (*Sc'*), graduated so as to read 0.1 mm., and the double pointer (*I*, *II*) on the wheel (*W'*) the increase in length can be obtained accurately, while this value can be obtained roughly by means of a linear scale hung near the thread on this side of the apparatus, but omitted from the figure for the sake of clearness. There is a curved guard (*G*) to protect the pointers.

The frame (*F*) requires more detailed description. It consists of a bow of heavy wire, 2.2 mm. thick and about 12 cm. in diameter, closed by a yoke (*Yk*) and suspended by a block of wood which holds four mirrors (*M*). These mirrors (fig. 2), each one 1.2 cm. in diameter (or better 1.0 cm.), are arranged in two pairs at right angles, and are held together by means of a piece of sheet metal (best of aluminum), which is cut to resemble roughly a cross and then bent into the form shown. These mirrors are held in place by fine wires and are labeled *A*, *B*, *C*, *D*. The yoke (*Yk*, fig. 3) is a curved piece of hard wood (about 5×1×0.6 cm.) and has fitted



FIGS. 1–4

over it a piece of "tin" (*t*), which is approximately U-shaped, with the "base" of the U back of the yoke. Its position on the yoke can be regulated by means of a peg on the small screw (*s*), only a little of which can be seen in fig. 3. This peg is between the yoke and the base of the U-piece. Another piece of "tin" (*r*) is hinged upon *t* by a pin, and has fastened to it by fine wire a rubber pad (*p*). Another rubber pad (*q*) is fastened to the yoke. These pads are pieces of 4 mm. rubber tubing (even smaller can be used for some purposes), and each has a groove cut a little more than halfway around it before it is secured in place. A slot in *r* fits over the screw (*s'*) when *r* is closed, and then the grooves on the two pads come together and make a place for holding the stem. A peg through the screw (*s'*) keeps this clamp closed. By adjusting the screws (*s* and *s'*) the correct amount of pressure required to hold the stem from slipping without interfering with its growth is obtained. This is easily determined by a few trials. The entire frame weighs about 20 gm. The clamp for holding the lower part of the stem used is constructed in the same way.

In order to keep tally on the number of complete revolutions which the stem makes in twisting, a black thread (the fine silk thread being white) is attached to the upper part of the bow of the frame, and, allowing plenty of slack, is then carried over a hook near the wheel (*W*). The number of times this is coiled (very loosely) about the silk gives the amount of twist roughly, while it is given exactly by means of the mirrors, telescope, and semicircular scale. For the sake of clearness this black thread also has been omitted from the figure.

One other device which, although imperfect, was found useful in studying intermediate points in the part of the stem used is here described and is illustrated in figs. 4 and 4*a*. I call it a "mirror clamp." It consists of two symmetrical halves (*a* and *b*) cut out of aluminum and bent into shape as shown. These halves are hinged together at one edge, and when closed form essentially a cube without a bottom. A mirror of quite thin glass, about 1 cm. square, is held in place on each side of the cube with bits of adhesive plaster. The clamp is opened by means of holders (*c* and *d*) on the two halves, and it is kept closed by means of the steel spring (*e*). On the top of each half there are two projections (*h*, *k* and *m*, *n*). Fig. 4*a* shows with enlargement how a piece of stout thread is placed on one pair of these. It is not tied, but the ends are twisted about each other several times (more than shown). On *h*, *k* two loops of this thread are placed, instead of one, and in such a way that the inner part on *m*, *n* comes between the inner parts of the two loops on *h*, *k* when the clamp is closed. A piece of fine copper wire (*f*), several cm. long, is attached to one-half of the clamp. This can be adjusted by bending so as to counterbalance the holders opposite. The entire device weighs somewhat over 1 gm. Since the mirrors are placed at some distance from the vertical axis, slight corrections are necessary for accurate work. In order to measure the growth in length of the point holding this clamp, a linear scale, fastened vertically, was used. With care this measurement could be made with fair accuracy.

In its simplest terms, torsional rigidity may be looked upon as "resistance to twisting." In earlier experiments it was estimated by balancing a measured deflection in the part of the vine used against a measured twist in a very fine wire. As this required additional apparatus, as the readings were rather difficult to make satisfactorily, and as the results were not very accurate, it will not be described in detail. The success of the present method, which is not open to these objections, depends on making the frame light, compact, and with small resistance to the air. In making a determination by the present method, the period of oscillation of the frame is timed. This is, in fact, a common method in physical laboratories. As may be learned from any textbook in physics,[3] the law governing this may be stated as follows: If a circular wire of length L and radius of cross-section R suspends a body whose moment of inertia is K, and if the coefficient of torsional rigidity of the material of this wire is n, then the period of oscillation in seconds of this body is given by the following equation: $T=(1/R^2)\sqrt{8\pi KL \div n}$. From this, $n=8\pi KL \div T^2R^4$. It is more convenient, however, to use the diameter (D) of the vine, and I always use the same frame and am dealing with comparative values only. Consequently, the expression actually used is $L \div T^2D^4$, which equals what may be called *the coefficient of rigidity*. This may be defined for our purposes as *the relative measure of the resistance offered to twisting through a unit angle of an average unit length*

[3] For example, Watson, W., A text-book of physics. Longmans, Green & Co. 1900. p. 205.

of vine per average unit diameter. As in most of the experiments no accurate measurements of the diameter were made, the expression more commonly used is $L \div T^2$. I shall call this simply *the rigidity*, or *the relative resistance to twisting through a unit angle of an average unit length of the vine.* Certain objections to these terms will be discussed later. As will be seen, they are not constant, but vary.

These experiments were performed in a greenhouse and have extended over several seasons. Generally speaking, conditions were found satisfactory for growth only during May, June, and the first part of July, at least in this particular greenhouse.

The apparatus is set up on a bench and leveled so that the upright is plumb. A weight placed on the base and wires from near the top of the standard to the roof of the greenhouse give the apparatus stability. By means of slots and screws in the top piece and in the arm of the clamp (*K*), adjustments are made so that the vertical line to be taken by the silk and the part of the vine used passes through the center of the semicircular scale. The proper weight is then applied to the silk, and the upper part of the growing internode near the tip is clamped in the frame. The lower part of this internode, or the upper part of the next internode, is then very carefully secured by the clamp (*Cl*).

Measurements of diameter were made by means of a gauge similar to one form of wire gauge. This consists of a pair of straight-edges, one of them graduated, held securely together so as to make a V with a very small angle. Usually many readings were taken (about 10–40), but irregularities in the stem prevented much accuracy. It was not found possible to make many such measurements in the case of the black bindweed. General observations of weather and temperature were recorded, but were found to be of only limited value.

Data and curves

Table I contains in an abridged form the data of a typical experiment. The dates and times of the readings are given with the corresponding lengths and the corresponding amounts of total twist in angular degrees. The average periods of oscillation of the frame are given. This value, in seconds, is obtained in each case by observing the length of time required for a certain number of oscillations (usually 50 or 100, occasionally 200), making usually 4 or 5 determinations in each case. The average diameters are given. In some cases these were not measured directly, but were obtained from the diameter curve. The calculated values of rigidity ($L \div T^2$) and of coefficient of rigidity ($L \div T^2D^4$) are also given.

TABLE I

FLOWERING BEAN

No.	Date	Time	Length = L in gm.	Twist in degrees	Period of oscillation in seconds $=T$	Diameter in mm. $=D$	D^4	Rigidity $=L \div T^2$	Coefficient of rigidity $=L \div T^2D^4$
1.....	6–4–18	1:15 P.M.	2.00	0	2.22	1.50	5.06	0.41	0.080
2.....	6–5–18	7:55 A.M.	3.22	62	2.06	1.56	5.93	0.76	0.128
3.....	6–5–18	7:22 P.M.	5.18	391	2.32	1.67*	7.78	0.96	0.124
4.....	6–6–18	11:25 A.M.	7.24	713	2.05	1.80	10.50	1.72	0.164
5.....	6–6–18	6:05 P.M.	8.35	894	1.91	1.85*	11.70	2.29	0.196
6.....	6–7–18	9:25 A.M.	9.58	1078	1.70	1.91*	13.30	3.32	0.250
7.....	6–7–18	8:00 P.M.	10.01	1128	1.00	1.90	13.01	10.01	0.770
8.....	6–8–18	2:57 P.M.	9.92	1108	0.75	......	....	17.60	......
9.....	6–8–18	5:55 P.M.	10.00	1105	0.72	1.92	13.60	19.30	1.419
10.....	6–9–18	7:20 P.M.	10.08	1102	0.65	1.96	14.75	23.86	1.617

* Value obtained from diameter curve: points *a*, *b*, and *c*, fig. 5.

In fig. 5 these data are presented in curves. In all cases abscissae represent lengths. It will be observed that in the twist curve there is relatively little slope at first, but that this slope increases later; and that at the end of the curve there is a slight but sudden and distinct drop. In other words, at first the internode twists only a little as it grows; later it twists faster; and, when the full length has been attained, there is a slight reverse twist. Note in table I that reading no. 8 shows a slight decrease in length. This was frequently observed at or near the end of growth in other experiments. It is probably due, for the most part at least, to a temporary shortening of the silk thread on account of changes in humidity. It may mean also a slight coiling of the internode. As it probably does not mean an actual shortening, this reading is not plotted in the curve. Reading no. 9 is also omitted from the twist curve.

The rigidity curve shows at first only a slight upward slope, but when the internode is approaching its full length there is a sudden and extensive upward turn in the curve. The coefficient of rigidity

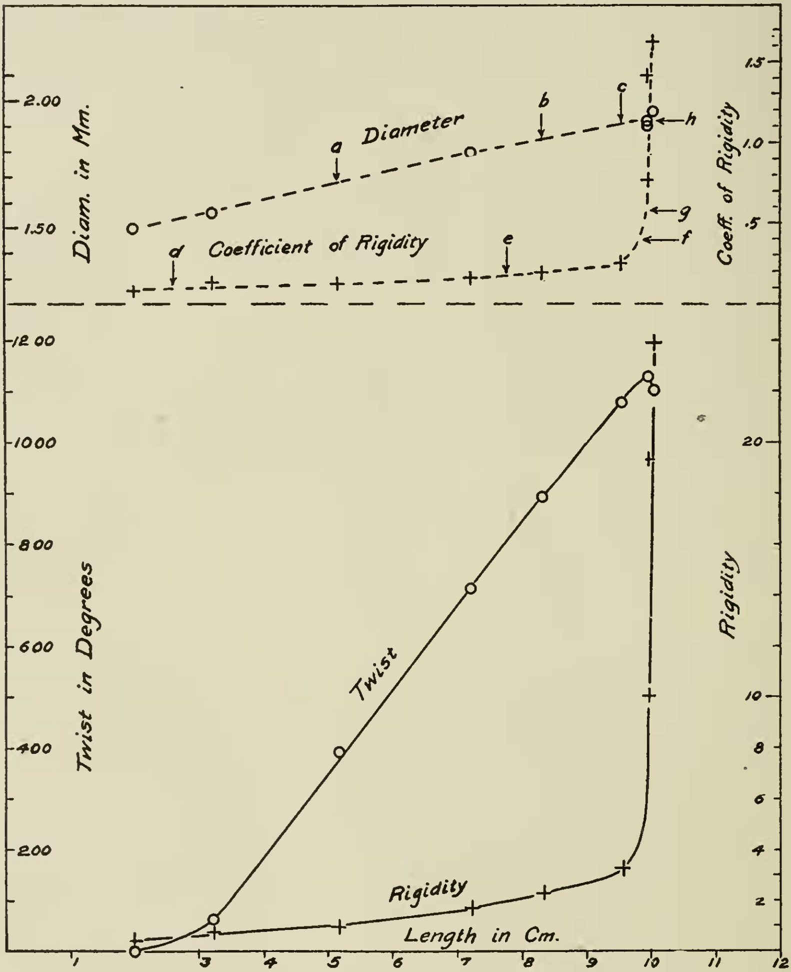


FIG. 5

curve shows the same general properties, but careful study shows that its first slope, that is, up to the point *e*, compared with the initial value of this coefficient, is much less than the ratio between the corresponding values in the rigidity curve. This demonstrates that increase in diameter accounts to a great extent for increase in rigidity during most of the internode's growth, but does not at all account for the final increase in rigidity.

Many experiments were performed under somewhat different conditions. The results of a few of these are presented graphically

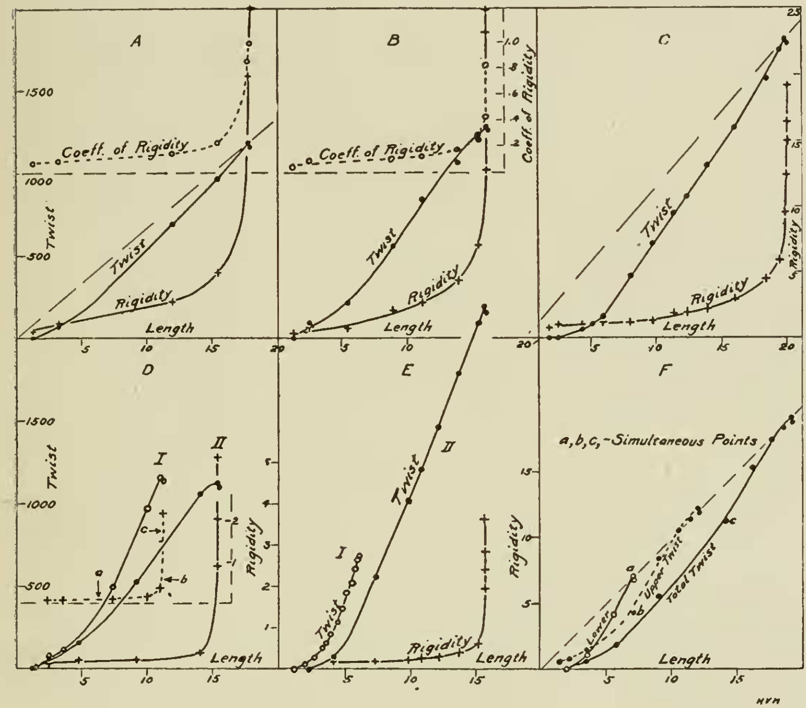


FIG. 6

on a smaller scale in fig. 6, while some of the important data are given for purposes of comparison in table II. The curves of twist, rigidity, and coefficient of rigidity show the same characteristics as those already outlined for fig. 5. It should be mentioned, however, that the final drops in the twist curves in fig. 6 have necessarily been more or less exaggerated. Curves *D*–I and *D*–II are for black bindweed, where the torsion is in the opposite direction from that in the flowering bean, being in the same sense as the thread of a right-handed screw in the latter, while it is in the same sense as that of a left-handed screw in the former. The rigidity curves for the bindweed are much smaller in dimensions than for the bean. It will also be noticed that differences in diameters account to a great extent for differences in rigidity curves in general.

Curve *E*–I is interesting in that it shows that when the healthy vine is limited in its growth by unfavorable conditions the same rules as to twisting apply. Even in this case there was, as a matter of fact, a slight reverse twist at the end, although the figure does not show it. On the other hand, under distinctly adverse conditions (as when the greenhouse became too hot and too dry), not only was the growth itself stunted, but the torsion was quite irregular. The resulting plant in such a case could hardly be regarded as healthy.

Curves *E*–II are also interesting. Here at the beginning of the experiment the growing tip was purposely removed, but not the leaf at the upper node, which was just above the clamp in the frame. This produced no apparent effect upon the two curves. On the other hand, in some experiments the vine just below the upper node was pinched accidentally, after which that internode died. In this experiment, however, it was observed that the stump above the upper node grew 2 or 3 cm. during the experiment and exhibited apparently a normal amount of twist. In the meantime a new bud appeared at this node.

One more interesting point is shown by curves *F*. Two adjacent internodes were fastened in the apparatus and were measured for length and twist in the usual way, while the behavior of the node between them was studied by means of the mirror clamp (fig. 4). From the resulting data three curves were obtained: one for the part below the node, one for the part above, and one for the total. These curves are plotted together and then a straight line is drawn from the "zero" point to the top of the total curve. The tops of the other two curves fall approximately on this line also. This shows that in a limited portion of the vine, where torsion is taking place freely, the final amount of torsion per unit length is uniformly distributed. If a single internode had been studied in this way, presumably a similar result would have been obtained. This

TABLE II

No.	Date of experiment	Species	Internode	Diam. at end of exp. in min.	Tension net wt. in gm.	Weather conditions	Curves	Remarks
1......	June 4 to 9, 1918	Flowering bean	7th on branch from first node	1.96	10	Largely cloud	Fig. 5	....
2*.....	May 31 to June 3, 1918	"	13th	2.25	10	Largely sun	*A* in fig. 6	Final twist = 66° per cm.
3......	May 26 to 31, 1918	"	11th	2.36	10	Largely cloud	*B* in fig. 6	Final twist = 79° per cm.
4......	May 10 to 20, 1918	"	5th and 6th	2.1	10	Mostly sun	*C* in fig. 6	Final twist = 90° per cm.
5......	June 29 to July 4, 1918	Black bind-weed	12th	1.0	5	Rain and sun	*D*–I in fig. 6	Twist opposite from bean
6......	June 26 to 29, 1918	"	17th and 18th	1.3	5	Mostly sun	*D*–II in fig. 6	Twist opposite from bean
7......	Sept. 21 to 30, 1915	Flowering bean	8th and 9th	About 1.0	13	Sun, rain, cloud	*E*–I in fig. 6	Growth under unfavorable conditions
8......	June 9 to 17, 1918	"	....	1.5	10	Mostly sun	*E*–II in fig. 6	Tip removed
9......	June 12 to 18, 1918	"	11th and 12th on branch at first node	2.1	10	Sun and cloud	*F* in fig. 6	Study of twist in 2 parts

* Nos. 2, 3, and 4 from same plant.

conclusion, however, does not hold for the vine as a whole. This is illustrated by the straight slope lines with curves *A* and *C*, fig. 6, which were obtained from widely separated parts of the same vine. Compare also the final twists per centimeter for nos. 2 and 4 in table II.

Lignification studies

The fact that increase in diameter does not account for the final development of rigidity has already been mentioned. It occurred

TABLE III

LIGNIFICATION TESTS; FLOWERING BEAN

No.	Internode	Length in cm. = L	Period in sec. = T	Diam. in mm. = D	$\frac{L}{T^2D^4}$	Amount of tissue stained with phloroglucin and HCl	Corresponding points on the coefficient of rigidity curve; fig. 5
1..	n*	1.3	1.92	1.5	.07	Only small vessels in vascular bundles	....
2..	n−1, upper half	1.9	0.93	2.2	.09	Same as in 1, only vessels larger	*d*
3..	n−1, lower half	1.9	0.53	2.5	.17	Vessels larger than in 2; narrow ring of xylem slightly stained	*e*
4..	n−2, middle of upper half	1.8	0.40	2.3	.40	A definite ring of well-stained xylem	*f*
5..	n−2, middle of lower half	1.8	0.40	2.1	.58	Xylem more heavily stained, that is, thicker walled elements	*g*
6..	n−3, upper half	4.0	0.47	2.0	1.14	Xylem still more heavily stained; more contrast between 6 and 4 than between 5 and 4	*h*

* The terminal part; the number of this internode was not counted and so is called *n*.

to the writer that studies in lignification might be useful. For this purpose rigidity and its coefficient were determined on adjacent parts of stems of the flowering bean and of the black bindweed, and free-hand sections from the middle of each specimen were treated with 5 per cent phloroglucin followed by strong HCl.[4] In this way the lignin was stained reddish violet. In tables III and IV the data are given for two such experiments. When the observa-

[4] CHAMBERLAIN, C. J., Methods in plant histology. University of Chicago Press. 1905. p. 62.

tions in table III are correlated with the points *d*, *e*, *f*, *g*, and *h* on the coefficient of rigidity curve in fig. 5, it is seen that the growing internode does not show much rigidity until there is considerable lignified tissue present. For correlation with table IV we choose the rigidity curve of *D*–I, fig. 6, because the final diameter in this

TABLE IV

LIGNIFICATION TESTS; BLACK BINDWEED

No.	Internode	Length in cm. = *L*	Period in sec. = *T*	Diam. in mm. = *D*	$\frac{L}{T^2}$	Amount of tissue stained with phloroglucin and HCl	Corresponding points on rigidity curve; fig. 6, *D*–1
1..	n*	1.1	7.47	0.70	0.02	Only a few small vessels	....
2..	n−1	1.7	5.03	0.85	0.07	Same as 1, only vessels larger	....
3..	n−2, upper half	2.0	4.39	0.90	0.10	Vessels still larger and better stained	*a*
4..	n−2, lower half	2.0	1.85	1.00	0.59	Vessels about as in 3; ring of well-stained sclerenchyma	*b*
5..	n−3, upper half	1.7	1.12	1.05	1.35	Sclerenchyma better stained; more of xylem stained	....
6..	n−3, lower half	1.75	1.00	1.05	1.75	Sclerenchyma still better stained; still more of xylem stained; more contrast between 6 and 4 than between 5 and 4	*c*

* The terminal part; the number of this internode was not determined and so is called *n*.

case is nearly the same as that in table IV. The points *a*, *b*, and *c* again demonstrate that increase in rigidity corresponds with development of lignified tissue.

Antidromous torsion

In the studies on antidromous torsion, a glass rod lubricated with vaseline was attached vertically to the apparatus, so that the frame was allowed to move upward freely but was prevented by this rod from rotating. At the same time the behavior of the midpoint of the part of the vine used was studied by means of the mirror clamp. It was found that this midpoint turned in the same direction as the frame would have done if it had been free to do so. In the case of the bean, for example, under favorable growing conditions the midpoint of an internode was found to twist through somewhat over 360°. In the meantime a reverse twist was produced in the upper part, which continued to grow in length after the lower part had stopped. In other words, *homodromous torsion* in the lower part overpowered the younger and less rigid upper part and produced *antidromous torsion* in it.

If the frame was released before the internode had stopped growing in length, the upper part recovered to a certain extent from its reverse twist. If this was not done until full growth was attained, it recovered but little or not at all. It does not seem worth while to give results in more detail at present, but it is planned to pursue these points further by modifications of the method.

A few experiments have been made with the first internode of the flowering bean when fastened in this apparatus. It is found to twist in the same direction as other internodes, but only to a limited extent (about 90° or less). Determinations of rigidity gave the same general results as for other internodes. Hop vines were studied to some extent. The indications are that the same general conclusions hold here also, but the experiments were not very complete.

Discussion

The question of reliability of measurements and of results is first to be considered. The errors in measuring increases in length are generally negligible compared with those in other measurements. The first length, however, can be measured only to within about one mm., and this error affects all other lengths, but to a much less extent. Only the first values of rigidity and its coefficient are very much affected by it. As already mentioned, when using the mirror clamp, corresponding lengths can be measured with only fair accuracy. A careful consideration of our readings of the twist shows that these are generally accurate to within 2 or 3°. Disturbing influences, such as air currents and imperfections in apparatus, give at times greater errors than these, and account, in part at least, for slight irregularities in the curves. Determinations of the period of oscillation are generally accurate to about 1 or 2 per cent. Since the square of this value is used in the calculations, this introduces an error of about 2–4 per cent in the values for rigidity. In the last part of each experiment care must be taken to have the part of the vine within the frame and above the upper clamp as nearly vertical as possible in order to avoid changes in the moment of inertia of the frame, and consequent error in the period of oscillation. Determinations of diameter are least accurate, only to about 3 or 4 per cent, and as the fourth power is used in these calculations, this introduces a further error of about 12–16 per cent in the values for coefficient of rigidity. Moreover, the vines are not perfectly circular in cross-section and are not of uniform texture, as would be the case with a metal wire. For this reason there are objections to the use of the terms rigidity and coefficient of rigidity, in that they do not have as definite values as in physics. When, however, these limitations are borne in mind, and it is remembered that they express relative average values only, it is believed that there should be no confusion. I believe that these errors do not vitiate the conclusions which I have drawn from the curves. It may be well to mention that similar rigidity curves were obtained when the former method of balancing twist in the vine against twist in a fine wire was used.

It may be objected that the material was studied under unnatural conditions, and that stretching introduces an unknown quantity. This is to a great extent true, but it is also true that many other investigations are made under unnatural conditions; for example, histological studies are usually made upon material that has been killed and stained. As a matter of fact, twining plants, when they can get necessary support otherwise, are sometimes observed to twist freely without much coiling or actual twining. This was observed, for example, several times in the greenhouse when a flowering bean grew near a tomato plant and found support among its leaves and branches. It must also be remembered that in ordinary twining the stem is probably subject to more or less tension. What effect, if any, is produced by the amount of tension used, and what effect, if any, the pressure of the clamps has upon the vine can be determined only by further studies.

The first part of the twist curve, which shows only a little slope, may be taken to correspond with that phase of growth which has to do largely with circumnutation, and in which there is but little twist. Torsion of the stem (but not twining proper) is generally regarded as due to internal forces. It is evident that these forces must reside in the primary tissues, while the final stability of the internode is due to the development of secondary, lignified tissues, corresponding with the last part of the rigidity curve. Apparently lignification stops these internal forces and "sets" the stem with whatever torsion it has acquired. It is very likely that if non-twining stems were studied in a similar way with reference to rigidity similar results would be obtained.

I have not gone into morphological details because I believe that the histology of twining plants with special reference to the points mentioned deserves a more careful study than it has been possible to give it thus far. Further experiments are necessary before any more general conclusions can be drawn.

Summary

The scarlet runner bean and the black bindweed have been studied with respect to torsion in a modified form of auxanometer. It is demonstrated that, as the internode grows in length, at first it twists but little, later it twists much more rapidly, and at the end of its growth in length there is a slight reverse twist. Rigidity, or "resistance to twisting," increases only slowly until near the end of growth in length, when there is a sudden and extensive increase. This final increase in rigidity accompanies the development of secondary, lignified tissues. If we prevent the frame holding the upper part of the internode from rotating, the lower part executes homodromous torsion, and by overpowering the upper part produces antidromous torsion in it. The first internode of the bean twists only a little when held in the apparatus. In a limited portion of the vine when free to twist, the amount of torsion per unit length is about constant, but this is not true of the vine as a whole.

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